

VERNAL POOL BLUE DICKS (*DICHELOSTEMMA LACUNA-VERNALIS*;
ASPARAGACEAE: BRODIAEOIDEAE) REVISITED

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ABSTRACT

Dichelostemma lacuna-vernalis L.W. Lenz was proposed in 1974 for populations of a diminutive *Dichelostemma* associated with vernal pool terrain. The author of *Dichelostemma* in the 1993 edition of *The Jepson Manual* did not accept the new species, reporting that the morphological and ecological characteristics of *D. lacuna-vernalis* were within the ranges for *D. capitatum* (Benth.) Alph.Wood. The purpose of this paper was to test the validity of *D. lacuna-vernalis* using a morphometric analysis of eighteen morphological characters in populations of *D. capitatum* and *D. lacuna-vernalis* sampled in the field and by comparing plants of both taxa grown under common garden conditions. The data were subjected to cluster analysis, principal components analysis, and discriminant analysis. The results of the analysis confirm the morphological distinctness of *D. lacuna-vernalis* and support its recognition as a separate taxon. Based on current taxonomic concepts in the Brodiaeoideae, this taxon is best recognized at subspecies rank, as *D. capitatum* subsp. *lacuna-vernalis* (L. W. Lenz) D.W. Taylor. Populations of *D. capitatum* subsp. *lacuna-vernalis* are distinguished by their short scapes (ca. 15 cm), inflorescences with one or two flowers, short (≤ 4 mm) perianth tubes, and outer perianth lobes that are ovate, decurrent at the base, and wider than the inner perianth lobes.

Key Words: California, *Dichelostemma*, geophyte, taxonomy, Themidaceae.

The genus *Dichelostemma* Kunth currently consists of five geophyte species endemic to the western USA and northern México (Pires 2002, Pires and Keator 2012). Phylogenetic studies place *Dichelostemma* in Themidaceae (Fay and Chase 1996; Fay et al. 2000; Pires et al. 2001; Pires and Sytsma 2002) and more recently in subfamily Brodiaeoideae of the Asparagaceae (Chase et al. 2009; Steele et al. 2012). These studies also indicate that *Dichelostemma* is not monophyletic; one species, *Dichelostemma capitatum* (Benth.) Alph.Wood, is sister to the clade that includes *Brodiaea* Sm. and the other four species of *Dichelostemma*.

Dichelostemma capitatum has been the subject of nearly perpetual taxonomic confusion since the early 19th century, so much so that Keator (1992) dubbed it a “problematic” species. It is the only hexandrous species in the genus, which prompted Baker (1871) to propose moving it to the genus *Muilla* S. Watson. On the same basis, Rydberg (1912) proposed placing the species in its own genus, *Dipterostemon* Rydb., into which he also placed three other taxa now treated as synonyms or subspecies of *D. capitatum*. Rydberg’s argument that the possession of six stamens was sufficiently diagnostic to warrant segregation of this new genus seemed weakly justified.

However, *D. capitatum* possesses multiple other characters that further differentiate it from other *Dichelostemma* species. Hoover (1940) observed that *D. capitatum* produces cormlets at the base of the corms and at the ends of short stalks, whereas all other species of *Dichelostemma* produce

cormlets only at the base of the corm. Keator (1968) noted many additional differences between *D. capitatum* and the other species of *Dichelostemma* in leaf width, pubescence of the scape, arrangement of tracheids in the stem, shape of the seed coat cells, and the seed germination pattern. Keator (1991) also noted that *D. capitatum* does not hybridize with other *Dichelostemma* species, whereas the other species hybridize with each other. In *D. capitatum*, the six stamens are united at the base of the filaments into a short staminal tube via fusion of the connective tissue, a feature not present in the other species of *Dichelostemma* (Lenz 1976). Moreover, the staminal tube possesses six lanceolate appendages that extend upward and cover the anthers and style, similar but not homologous to the corona found in other species of *Dichelostemma*, which is an extension of the perianth (Lenz 1976). Berg (1996) proposed resurrecting *Dipterostemon* on the basis of embryology. Although the embryology of *Brodiaea* and *Dichelostemma* is quite similar, the inner integument of the ovule of *D. capitatum* consists of two cell layers, similar to that of *Muilla* and *Triteleia* Douglas ex Lindl., but different from the multilayered inner integument that represents a synapomorphy of *Brodiaea* and the other *Dichelostemma* species (Berg 1978, 1996, 2003). The morphological evidence for recognizing *Dipterostemon* is fully supported by the molecular data, which show that *Dichelostemma* is only monophyletic if *D. capitatum* is excluded (Pires et al. 2001; Pires & Sytsma 2002; Nguyen et al. 2008; Steele et al. 2012).

Although *D. capitatum* exhibits a high degree of morphological variation, only a single infraspecific taxon within *D. capitatum* is currently recognized, *D. capitatum* subsp. *pauciflorum* (Torr.) Keator. However, Lenz (1974) proposed that populations of diminutive *Dichelostemma capitatum* associated with vernal pool terrain be recognized as a new species, *D. lacuna-vernalis* L.W. Lenz. Lenz characterized the new species as morphologically similar to *D. capitatum* but differing by having broad, keel-less leaves, 1–3-flowered inflorescences, shorter scapes, and smaller bracts. Lenz also indicated that *D. lacuna-vernalis* occurred in different habitats than *D. capitatum*, although he was not specific about the habitat differences. Keator (1991) did not accept the new taxon, reporting that the morphological and ecological characteristics of *D. lacuna-vernalis* were within the ranges for *D. capitatum*. He suggested that smaller stature and fewer flowers were a result of environmentally-induced phenotypic plasticity, a consequence of stress from growing in seasonally saturated soils, i.e., that plants referable to *D. lacuna-vernalis* were simply on the low end of the normal range of size variation for *D. capitatum*. In the treatment of *Dichelostemma* for *The Jepson Manual*, Keator (1993) placed *D. lacuna-vernalis* in synonymy with *D. capitatum*. Because *D. lacuna-vernalis* was based on a single population, and because Lenz' characterization of the differences between *D. capitatum* and *D. lacuna-vernalis* was very general, and the protologue lacked a key to differentiate between the species, perhaps Keator was justifiably conservative in not recognizing *D. lacuna-vernalis*. Pires (2002) and Pires and Keator (2012) concurred with Keator's treatment of *D. capitatum* but acknowledged that further study of the taxon was warranted.

In March 2007, I encountered a population of diminutive *Dichelostemma* plants in Butte County growing sympatrically with a population of typical *D. capitatum*. The plants matched Lenz' description of *D. lacuna-vernalis*, and on further inspection, I found that in addition to their short stature and few-flowered inflorescences, the perianth tubes were very short, a feature that Hoover (1940) had earlier noted in depauperate plants of *D. capitatum*. In addition, I observed that the outer perianth lobes were broadly ovate with cordate bases, unlike the oblong, truncate-based perianth lobes of typical *D. capitatum*. These observations prompted me to initiate a closer comparison of *D. capitatum* and *D. lacuna-vernalis*.

Keator's (1991) hypothesis that *D. lacuna-vernalis* does not warrant taxonomic recognition rested on two assumptions: first, that morphological variation in *D. capitatum* is continuous from robust plants to depauperate plants, i.e.,

there is no morphological discontinuity that that reliably distinguishes *D. lacuna-vernalis* from *D. capitatum*; and second, that the primary source of variation among populations stems from a response to environmental factors, i.e., that the morphology of plants assignable to *D. lacuna-vernalis* is the result of phenotypic plasticity. The purpose of this study is to test Keator's hypothesis by addressing each of the underlying assumptions: 1) does the range of morphological variation in populations assignable to *D. lacuna-vernalis* overlap continuously with that of *D. capitatum*; and 2) do plants from *D. capitatum* populations and from *D. lacuna-vernalis* populations differ morphologically when grown under the same environmental conditions? To answer the first question, I sampled populations of *D. capitatum* throughout northern California, including populations assignable to *D. lacuna-vernalis* on the basis of characters proposed by Lenz (1974), and subjected the data to a morphometric analysis. To answer the second question, I collected corms from populations of both putative taxa, grew them in pots in a common garden, and compared their morphology both to each other and to their source populations.

METHODS

Population Sampling

Between 2007 and 2014, I sampled 59 *Dichelostemma* populations in northern California, primarily from the eastern Sacramento Valley and adjacent Sierra Nevada foothills, but also from the interior North Coast Ranges and other scattered locations (Appendix 1). For each population, plants were collected with intact corms or were placed in water to prevent the flowers from wilting before measurements were made. I measured scape height, maximum leaf width, number of flowers, maximum bract length, and maximum pedicel length. I dissected one flower from 10–30 plants in each population, using flowers at approximately the same stage of anthesis, to minimize variation due to any change in flower size from the beginning to the end of anthesis. I measured 13 floral characters and noted the shape and position of the floral parts.

Common Garden Plants

I grew plants in a common garden from corms collected from the populations of *D. capitatum* and *D. lacuna-vernalis* sampled for the morphological characters. The corms were planted in 8-inch pots using a commercial potting mix. Plants were grown together outside under conditions of ambient temperature, light, and rainfall, with occasional supplemental watering. I measured the

same set of morphological characters for the garden-grown plants that were sampled for populations in the field. I also measured corm characteristics, including the number and size of cormlets produced.

Morphological Analysis

Sixteen populations were assigned to *D. lacuna-vernalis* (L01–L16 in Appendix 1) based on their occurrence in vernal pool terrain and on the following diagnostic characters from Lenz (1974) and from my own personal observations: stems less than 2 dm tall; inflorescence with 1–3 flowers; perianth tube less than or equal to 4 mm long; and, outer perianth lobes broadly ovate with cordate bases. The other 43 populations were assigned to *D. capitatum* (C01–C43 in Appendix 1).

The field-collected data were analyzed using cluster analysis, principal components analysis (PCA), and discriminant analysis (DA). The cluster analysis and PCA were performed using the character means from each population (data matrix provided in Appendix 2), and the DA used the individual measures from each plant sampled. Prior to the analysis, the data were standardized by subtracting the mean of each variable and dividing by the standard deviation. The cluster analysis employed Ward's method and Euclidean distances. The DA was first performed using two groups, one consisting of plants assigned to populations of *D. lacuna-vernalis* and the second consisting of the plants assigned to populations of *D. capitatum*. The DA employed a forward stepwise analysis to identify characters with the highest discriminant power. A classification tree analysis was performed to further test the predictive value of each character and to determine the split between values for *D. capitatum* and *D. lacuna-vernalis*. All statistical tests were carried out using the SYSTAT 13 statistics program (SYSTAT Software, Chicago, IL).

RESULTS

Morphological Analysis

Cluster analysis. The cluster analysis found that the populations form several clusters that are largely distinct (Fig. 1). The first cluster (Group 1) includes 21 populations of *D. capitatum* from scattered locations throughout northern California (C1–C21). The second cluster (Group 2) includes the *D. lacuna-vernalis* populations (L1–L16) but also includes 22 populations of *D. capitatum* that share some character states with *D. lacuna-vernalis* and others with *D. capitatum* populations in Group 1. Group 2 is comprised of two subclusters, the first of which (Group 2A)

includes populations of *D. capitatum* from the northern Sierra Nevada foothills and the interior North Coast Ranges and two (C22–C43) populations of *D. lacuna-vernalis* (L15, L16), and the second of which (Group 2B) contains the remaining populations of *D. lacuna-vernalis* (L1–L14).

Principal components analysis. The plots of the principal component scores graphically illustrate the morphological distinctiveness of *D. lacuna-vernalis* (Fig. 2a, b). Moreover, the PCA found that the two groups of *D. capitatum* populations found in the cluster analysis also show little overlap. The first principal component (Factor 1), which accounts for 49.2% of the variation, appears to be a general size factor (Table 1). Populations of the diminutive *D. lacuna-vernalis* are grouped at the low end of Factor 1. The more robust populations of *D. capitatum*, which correspond to Group 1 in the cluster analysis, are grouped at the high end of Factor 1, and populations of *D. capitatum* in Group 2a in the cluster analysis are in an intermediate position (Fig. 2a). The second principal component, which accounts for 21.8% of the variation, is also a size factor, but it loads primarily on the length and width of the petals. Factor 2 provides little separation of the three groups. The third factor, which accounts for 13.8% of the variation, loads primarily on ovule number but also appears to be a function of the relative lengths of the outer perianth lobes and the style. The *D. capitatum* populations corresponding to Group 2a in the cluster analysis are differentiated from *D. lacuna-vernalis* and the more robust *D. capitatum* populations (Group 1) along the axis of Factor 3 and are not in an intermediate position (Fig. 2b).

Discriminants analysis. The DA for all individuals from all populations found *D. lacuna-vernalis* to be morphologically distinct from *D. capitatum* (Wilks' $\lambda = 0.224$, $df = 13$, 1294, $P < 0.001$). Thirteen variables contributed significantly to the discriminant function, explaining 78% of the variation (Table 2). The DA correctly classified 98% of all individuals, with 99% of the *D. lacuna-vernalis* individuals correctly classified. Among the plants grouped with *D. capitatum*, 98% of the individuals were correctly classified; of the 18 misclassified individuals, 16 came from the small-flowered Interior North Coast Range populations. Variables with the highest loadings were length of the perianth tube, style length, width of the outer perianth lobes, scape height, appendage length, and plant height (Table 2). A DA conducted using just the first five variables in Table 2 was nearly as successful as the full model (Wilks' $\lambda = 0.260$, $df = 5$, 1306, $P < 0.001$), correctly classifying 97% of all individuals,

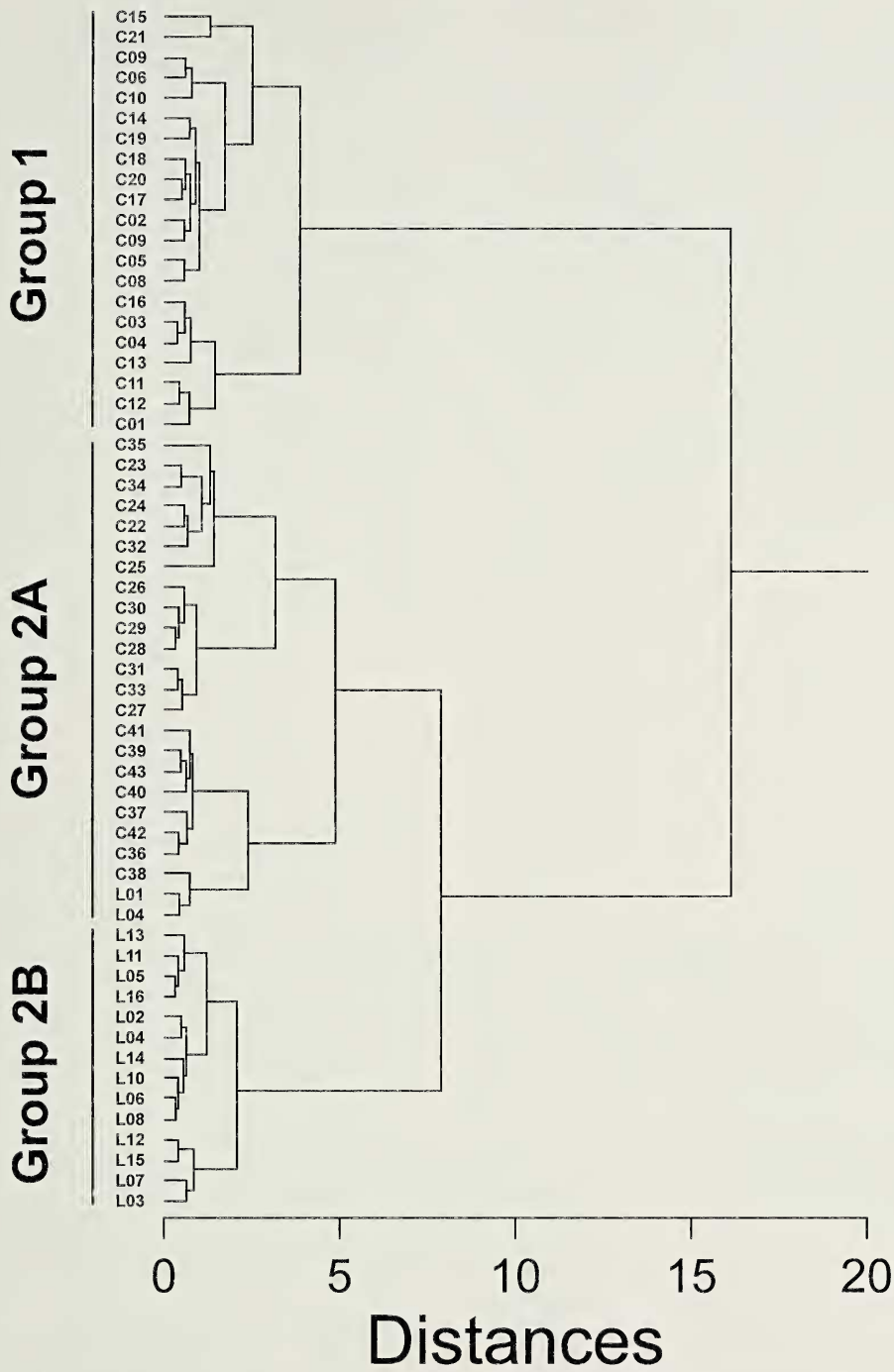


FIG. 1. Cluster tree for 42 populations of *D. capitatum* and 16 populations of *D. lacuna-vernalis*, based on cluster analysis of the means of 18 characters. Group 1 includes 21 populations of *D. capitatum* from scattered locations throughout northern California (C1–C21), and Group 2 includes *D. lacuna-vernalis* populations (L1–L16) and 22 populations of *D. capitatum* (C22–C42) from the northern Sierra Nevada foothills and inner North Coast Ranges. Population codes refer to voucher specimens cited in Appendix 1.

including 95% of the *D. lacuna-vernalis* individuals and 98% of the *D. capitatum* individuals.

Morphological comparisons. The cluster analysis, PCA, and DC all show that *D. lacuna-vernalis*

is morphologically distinct from *D. capitatum*. Although the range of values for each quantitative character measured for *D. lacuna-vernalis* overlaps with those for *D. capitatum*, the means for most characters are significantly smaller than

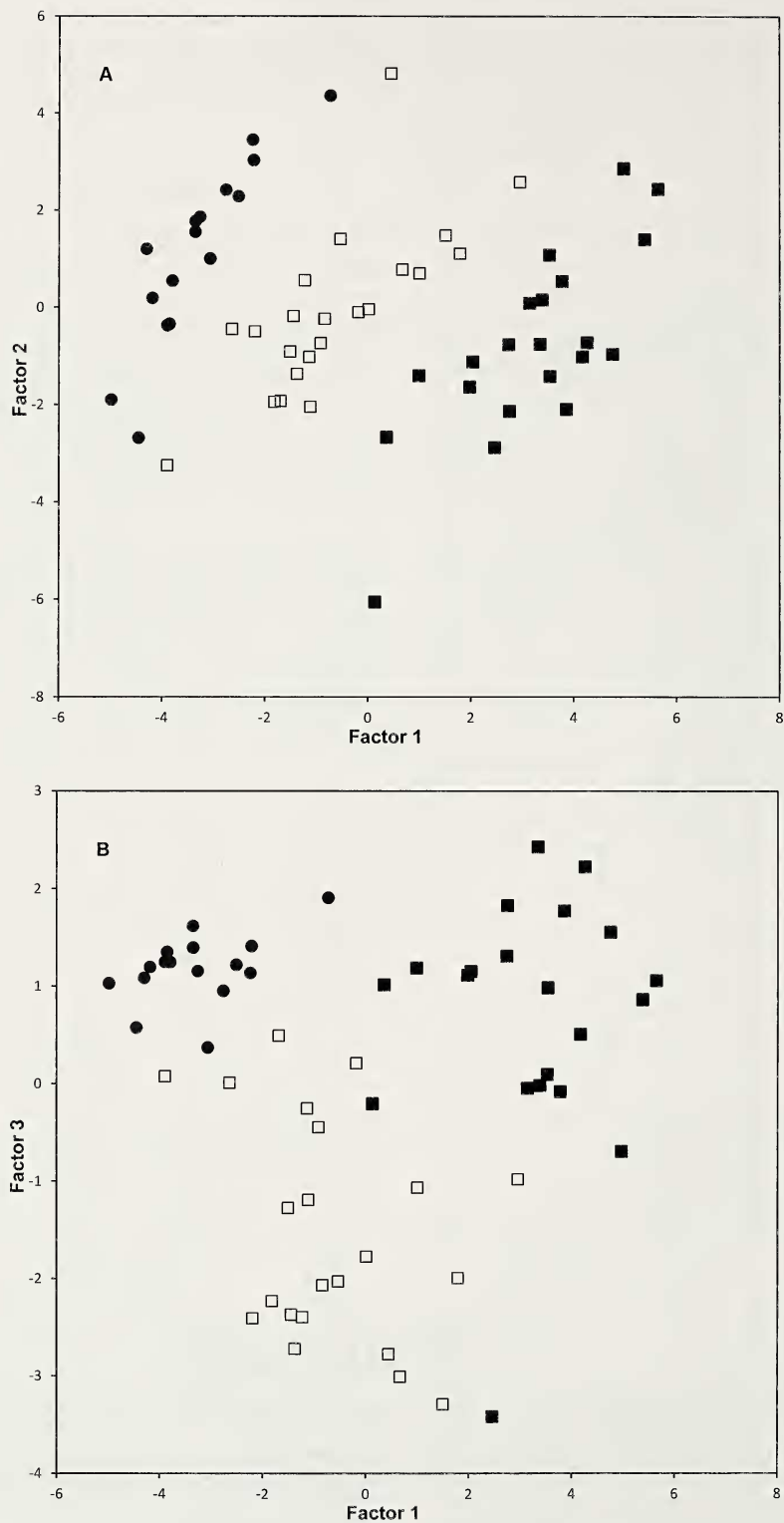


FIG. 2. Plot of factor scores from principal components analysis of 42 populations of *D. capitatum* and 16 populations of *D. lacuna-vernalis*, based on the means of 18 morphological characters. A. Factor 1 vs. Factor 2. B. Factor 1 vs. Factor 3. Closed squares = *D. capitatum* populations in cluster analysis Group 1, open squares = *D. capitatum* populations in cluster analysis Group 2, closed circles = *D. lacuna-vernalis*.

TABLE 1. RESULTS OF THE PRINCIPAL COMPONENTS ANALYSIS OF 59 POPULATIONS OF *DICHELOSTEMMA CAPITATUM* AND *D. LACUNA-VERNALIS*, BASED ON 18 MORPHOLOGICAL CHARACTERS.

Variable	Factor 1	Factor 2	Factor 3
Scape height	0.826	−0.278	0.082
Leaf width	0.792	−0.114	0.280
Flowers	0.825	−0.404	0.244
Bract length	0.917	−0.039	0.195
Pedicel length	0.861	−0.244	0.306
Perianth tube length	0.869	−0.225	−0.321
Outer lobe length	−0.118	0.735	−0.594
Inner lobe length	0.186	0.814	−0.360
Outer lobe width	−0.495	0.790	0.232
Inner lobe width	0.244	0.826	0.259
Appendage length	0.913	0.203	−0.223
Outer filament length	0.379	0.733	0.363
Inner filament length	0.615	0.454	0.462
Outer anther length	0.723	0.348	−0.374
Inner anther length	0.895	0.178	−0.174
Ovary length	0.940	0.063	0.148
Style length	0.773	0.065	−0.569
Ovules	−0.127	0.328	0.772
Eigenvalues	8.856	3.928	2.490
% of total variance explained	49.2	21.8	13.8

those for *D. capitatum* (Table 3), and the distribution of values is non-unimodal. The most readily observed differences between *D. lacuna-vernalis* and *D. capitatum* are the very short perianth tube (relative to the lobes) and the ovate (vs. oblong) outer perianth lobes that are wider than the inner lobes (Fig. 3). Other characters, such as short stature and few flowers per scape, are also found in *D. capitatum* populations that cluster in Group 2a. Although Lenz (1974) characterized the leaves of *D. lacuna-vernalis* as quite broad, the leaves of field collected plants were narrower than those of *D. capitatum*.

Based on the DA, scape height, perianth tube length, width of the outer perianth lobe, appendage length, and style length are the most useful characters for discriminating between *D. lacuna-vernalis* and *D. capitatum* (Table 2). The classification tree analysis was used to determine the nodal values for each character and to construct a matrix for differentiating between *D. capitatum* and *D. lacuna-vernalis* (Table 4). In addition, although flower number did not contribute significantly to the DA, it also appears to be a useful discriminator. Two characters not included in the DA, the ratio of the lengths of the perianth tube and perianth lobe and the relative width of the inner and outer perianth lobes, were also found to be highly predictive. Overall, the eight characters presented in Table 4 unambiguously assigned 89% of the sample individuals to the correct taxon, including 98% of the *D. lacuna-vernalis* individuals and 86% of the *D. capitatum* individuals. As might be expected from the cluster analysis, almost all of the misclassified individuals (having 5 or more characters in ranges for *D. lacuna-vernalis*) or ambiguous (having 4 characters in ranges for *D. capitatum* and 4 in ranges for *D. lacuna-vernalis*) were members of *D. capitatum* Group 2a. When all of the individuals in a population were considered together, all of the *D. lacuna-vernalis* populations were correctly classified, and only two of the 43 *D. capitatum* populations were misclassified. Most individuals in one *D. capitatum* population from the Sierra Nevada foothills (C25) were classified as *D. lacuna-vernalis*; these plants were small-statured and few-flowered but had large flowers. Another *D. capitatum* population from serpentine chaparral in the Interior Coast Range (C40) had many individuals classified as *D. lacuna-vernalis*; these plants were small-statured

TABLE 2. SUMMARY OF STEPWISE DISCRIMINANT ANALYSIS OF 18 CHARACTERS MEASURED FOR 1308 FIELD SAMPLED *DICHELOSTEMMA CAPITATUM* AND *DICHELOSTEMMA LACUNA-VERNALIS* INDIVIDUALS, INCLUDING THE STRUCTURE MATRIX CORRELATIONS BETWEEN CHARACTERS AND THE CANONICAL DISCRIMINANT FUNCTION SCORE. Five characters (flower number, bract length, pedicel length, length of the outer filament, and length of the inner anther) did not contribute significantly to the discriminant function.

Step	Character	Wilks' λ	Approximate F-ratio	Approximate p-value	Correlation coefficient
1	Perianth tube length	0.451	1,592.623	<0.001	0.841
2	Outer lobe width	0.355	1,188.106	<0.001	−0.686
3	Ovule number	0.313	954.301	<0.001	−0.586
4	Inner lobe width	0.272	871.634	<0.001	−0.143
5	Outer lobe length	0.26	742.549	<0.001	−0.012
6	Scape height	0.254	637.558	<0.001	0.634
7	Inner lobe length	0.247	567.402	<0.001	0.016
8	Appendage length	0.239	516.051	<0.001	0.634
9	Inner filament length	0.229	485.286	<0.001	0.021
10	Style length	0.226	443.462	<0.001	0.788
11	Ovary length	0.225	405.686	<0.001	0.488
12	Outer anther length	0.224	373.389	<0.001	0.348
13	Leaf width	0.224	345.117	<0.001	0.364

TABLE 3. MEANS AND RANGES FOR 19 CHARACTERS MEASURED IN FIELD-COLLECTED INDIVIDUALS OF *DICHELOSTEMMA CAPITATUM* AND *D. LACUNA-VERNALIS*. Within each row, means with different superscripts differ significantly (ANOVA, $P < 0.05$).

	<i>Dichelostemma capitatum</i>			<i>Dichelostemma lacuna-vernalis</i>		
	n	Mean	Range	n	Mean	Range
Height	881	27.6 ^a	3.1–64.3	378	14.4 ^b	4.4–26.1
Outer leaf width	870	7.2 ^a	2.5–25.0	378	5.3 ^b	2.2–12.5
Flowers	883	5.0 ^a	1–25	399	1.7 ^b	1–5
Bract length (maximum)	846	13.5 ^a	6.5–30.0	376	9.9 ^b	4.8–16.0
Pedicle length (maximum)	850	5.1 ^a	1–20.0	377	2.6 ^b	0.7–6.0
Perianth length	1016	15.9 ^a	10.8–22.9	387	13.6 ^b	9.8–17.8
Tube length	1024	5.8 ^a	3.2–10.3	390	3.6 ^b	2.0–6.0
Lobe length (outer)	829	11.1	7.0–16.5	338	11.4 ^b	7.5–14.6
Lobe length (inner)	1158	10.1	6.2–15.5	400	10.0 ^b	6.3–13.3
Lobe width (outer)	857	5.4 ^a	2.9–9.1	374	7.1 ^b	4.0–9.8
Lobe width (inner)	858	5.6	3.2–9.0	374	5.9 ^b	3.2–9.0
Appendage length	836	6.1 ^a	3.7–9.0	372	4.9 ^b	3.0–6.7
Filament length (outer)	829	2.6	1.4–5.2	367	2.7 ^b	1.5–3.8
Filament length (inner)	828	1.7	0.7–3.7	367	1.7 ^b	0.5–2.8
Anther length (outer)	829	2.4	1.0–4.0	367	2.1 ^b	1.2–3.0
Anther length (inner)	828	3.9	2.5–6.2	367	3.4 ^b	2.4–4.5
Ovary length	836	4.1 ^a	2.4–6.1	366	3.5 ^b	2.0–5.0
Style length	835	6.0 ^a	3.3–9.3	366	3.9 ^b	2.5–5.6
Ovules per ovary	862	29.6 ^a	9–54	367	38.2 ^b	21–60

and small-flowered, but the floral proportions were more similar to those of *D. capitatum*. One unanticipated result of this analysis was that among the sampled populations of *D. capitatum* there are two morphologically distinguishable forms. Both forms have long perianth tubes (relative to the lobes) and long styles.

However, populations in cluster analysis Group 1 generally have longer scapes and produce many more flowers per scape than populations in Group 2a. As suggested by the cluster analysis, plants in Group 2a populations are more similar in some respects to *D. lacuna-vernalis* than to Group 1 populations. Plants in Group 2a



FIG. 3. Flowers of *D. capitatum* (left, center), and *D. lacuna-vernalis* (right). The outer perianth lobes of *D. capitatum* populations in cluster analysis Group 2 (center) are decurrent at the base, which distinguishes them from populations in Group 1 (left). Scale bar = 5 mm.

TABLE 4. CHARACTER MATRIX FOR DIFFERENTIATING BETWEEN *DICHELOSTEMMA CAPITATUM* AND *D. LACUNA-VERNALIS*.

Character	<i>Dichelostemma capitatum</i>	<i>Dichelostemma lacuna-vernalis</i>	Percent of samples correctly classified
Scape height	>20 cm	≤20 cm	78.80%
Flower number	>2	≤2	83.50%
Perianth tube length	>4.1 mm	≤4.1 mm	93.20%
Ratio of tube length to lobe length	Tube length ≤ 2× lobe length	Tube length > 2× lobe length	85.90%
Outer perianth lobe, width	≤6.2 mm	>6.2 mm	82.50%
Relative width of inner and outer perianth lobes	Inner ≥ outer	Inner < outer	79.00%
Appendage length	>5.2 mm	≤5.2 mm	79.70%
Style length	>4.5 mm	≤4.5 mm	80.50%

populations and in *D. lacuna-vernalis* populations have ovate ovaries (vs. urn-shaped in Group 1), perianth lobes that spread from the tubes at different levels (vs. from the same level in Group 1), and outer perianth lobes that are decurrent down the perianth tube, below the base of the inner perianth lobes, for one to three mm (vs. not or decurrent less than one mm in Group 1). In other respects, such as scape length, leaf width, and flowers per scape, Group 2a populations of *D. capitatum* are intermediate between Group 1 populations and *D. lacuna-vernalis*. In Group 1 populations of *D. capitatum*, the inner perianth lobes are wider than the outer perianth lobes, but in Group 2a populations of *D. capitatum*, the inner and outer perianth lobes are the same width, on average.

Common Garden Plants

Plants grown in a common garden from corms collected from populations of *D. capitatum* and *D. lacuna-vernalis* maintained their distinctive morphology (Fig. 4). As in the field-collected samples, pot-grown individuals from populations of *D. lacuna-vernalis* were shorter, produced fewer flowers per scape, had shorter perianth tubes, and had broader perianth lobes than pot-grown individuals from populations of *D. capitatum*. Moreover, pot-grown individuals from populations of Group 2a populations of *D. capitatum* maintained their differences and similarities to Group 1 populations of *D. capitatum* and *D. lacuna-vernalis*.

Several other differences between *D. capitatum* and *D. lacuna-vernalis* were evident in pot-grown plants that were not readily apparent in the field. *Dichelostemma lacuna-vernalis* corms produced few cormlets, with only 44.8% of the corms producing cormlets (1.2 cormlets/corm, range 1–3). In contrast, 60.9% of *D. capitatum* corms produced cormlets (2.3 cormlets/corm, range 1–6). *Dichelostemma lacuna-vernalis* also is capable of producing scapes from smaller corms than *D. capitatum*. In *D. lacuna-vernalis*, 46.4% of corms 8–11 mm in diameter produced flowering scapes,

and 85.6% of corms 11–14 mm in diameter produced flowering scapes. In *D. capitatum*, only 15.5% of corms 8–11 mm in diameter produced flowering scapes, and only 59.3% of corms 11–14 mm in diameter produced flowering scapes. Moreover, *D. lacuna-vernalis* averaged 2.7 scapes per corm, and larger corms produced up to 8 scapes. *Dichelostemma capitatum* usually produced a single scape and rarely produced more than two scapes per corm (1.7 scapes per corm, range 1–6).

DISCUSSION

Dichelostemma capitatum is a broadly circumscribed species that consists of multiple cytotypes, but there has been little support from botanists for the recognition of infraspecific taxa, despite being widely distributed in the southwestern U.S. and northern México, occurring in a broad range of habitats, and exhibiting a high degree of morphological variation (Keator 1968, 1992). Keator (1968) sampled extensively among populations of *D. capitatum* throughout much of its range to determine whether combinations of morphological characters occurred together consistently enough to warrant formal recognition of segregate taxa. Although he found that that chromosome number differed substantially among populations (*n* = 9, 18, 27, and 36), he also found that the cytotypes generally were not morphologically distinguishable, except that diploid cytotypes sometimes had smaller flowers. Keator concluded that there were no character complexes by which to distinguish between cytotypes nor by which geographic races could be differentiated, further stating that “[s]uch characters as flower color, bract shape and color, and pedicel length are variable within populations to such an extent that their use for taxonomic or correlative purposes seems impossible (Keator 1968, p. 376).” Keator (1992) characterized the inability to utilize morphological data to elucidate ecological or evolutionary relationships within *D. capitatum* as “problematical.” However, Keator’s analysis was based on a

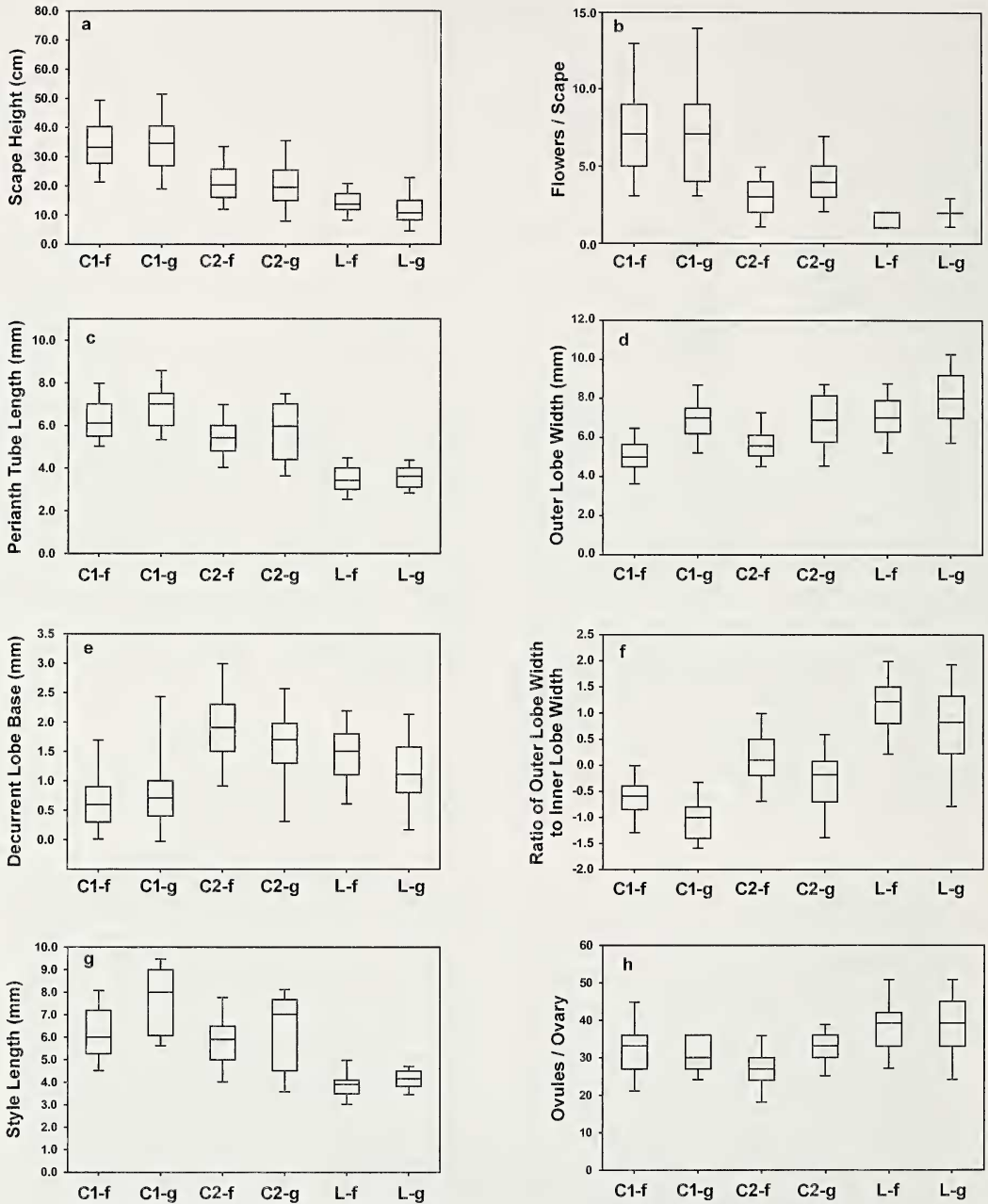


FIG. 4. Box plots comparing morphological characters measured in *Dichelostemma capitatum* and *D. lacuna-vernalis*. A) scape height in cm; B) flowers per scape; C) perianth tube length in mm; D) outer perianth lobe width in mm; E) length of decurrent base of outer perianth lobe in mm; F) ratio of outer lobe width to inner lobe width; G) style length in mm; H) ovules per ovary. The boxes represent the second and third quartiles, with the central horizontal lines representing the median; the upper and lower whiskers represent the 95th and 5th percentiles, respectively; outliers are not shown. C1-f = *D. capitatum* Group 1 cluster analysis populations, field collected individuals; C1-g = *D. capitatum* Group 1 populations, garden-grown individuals; C2-f = *D. capitatum* Group 2 populations, field collected individuals; C2-g = *D. capitatum* Group 2 populations, garden-grown individuals; L-f = *D. lacuna-vernalis*, field collected individuals; L-g = *D. lacuna-vernalis*, garden-grown individuals.

limited set of floral characters and did not employ a multivariate statistical approach.

Keator (1968, 1991), like Hoover (1940) before him, attributed morphological variation in *D. capitatum* to environmental plasticity. Both

authors rejected *Brodiaea insularis* Greene (= *Dichelostemma insulare* [Greene] Burnham), a taxon based on robust populations from the Channel Islands, citing the common occurrence of robust individuals in many mainland populations, when

observed growing under favorable conditions. Both authors cautiously recognized *D. capitatum* var. *pauciflorum* (Torr.) Hoover (= *D. capitatum* subsp. *pauciflorum* [Torr.] Keator) from desert areas of the southwestern U.S. and northern México, noting the presence of populations morphologically intermediate between var. *pauciflorum* and “typical” *D. capitatum*. Keator’s caution in recognizing other taxa within *D. capitatum* is consistent with the tradition among botanists that morphologically similar polyploid cytotypes are rarely named and considered as species separate from their diploid progenitors, primarily because of the practical aspects of differentiating between them in the field or herbarium (Judd et al. 2007; Soltis et al. 2007).

The results of the present study demonstrate that, contrary to Keator’s conclusion, the range of morphological variation in populations assignable to *D. lacuna-vernalis* does not overlap continuously with that of *D. capitatum*. Morphological variation is not continuous in *D. capitatum*, and variation within populations is much less than among populations. In each of the populations sampled for this study, individuals expressed a discrete range of morphological variation, not the full spectrum of possible phenotypes. Some groups of populations are morphologically more similar to each other than to other groups, i.e., character complexes exist by which groups of populations can be differentiated. Moreover, plants referable to *D. lacuna-vernalis* are not simply on the low end of the normal range of size variation for *D. capitatum*. Scape height, flowers per scape, perianth tube length, and style length in *D. lacuna-vernalis* are clearly outside the normal range for *D. capitatum* (Fig. 4a, b, c, g). Perianth tube length is rarely more than 4 mm in *D. lacuna-vernalis* and very rarely less than 4 mm in *D. capitatum* (Figs. 3, 4c). Also, not all characters are smaller in *D. lacuna-vernalis*; the outer perianth lobes are generally wider, not narrower, than those of *D. capitatum* (Fig. 4d), and the outer perianth lobes are wider than the inner perianth lobes (Fig. 4f). In *D. capitatum*, the perianth lobes are of equal width or the inner lobes are wider than the outer. In contrast to *D. lacuna-vernalis*, populations of *D. capitatum* with short perianths (i.e., populations C37–C43) have longer perianth tubes than *D. lacuna-vernalis* but relatively shorter perianth lobes.

Keator’s second objection to recognizing *lacuna-vernalis*, his belief that the smaller size of many characters in *D. lacuna-vernalis* is simply a plastic response to growing in waterlogged, clay soils, is not supported by the results of the common garden study. *Dichelostemma lacuna-vernalis* individuals maintain their small stature, few flowers, and other diagnostic characteristics, and *D. capitatum* individuals maintain their

larger stature and many flowers, when grown under identical conditions. Moreover, if the distinctive morphology of *D. lacuna-vernalis* was simply due to environmental conditions, then populations of *D. capitatum* growing in heterogeneous environments should contain a mixture of plants with both morphologies, and individuals with characteristics of *D. lacuna-vernalis* could be expected to occur in any part of the range for *D. capitatum*. Instead, *D. lacuna-vernalis* plants occur in discrete populations within a well-defined geographic distribution along the western base of the Sierra Nevada foothills and adjacent Great Valley, in a narrow elevation band between 30 and 270 m (Fig. 5).

That some of the variation observed in *Dichelostemma* populations may be environmentally induced is not in dispute. In other species in Brodiaeoideae, several characters, such as scape height and the number and size of cormlets produced, are influenced by moisture availability, temperature, or plant density (Niehaus 1971; Han et al. 1991; Coccozza et al. 2000). Corm size, which is a function of age and other factors, such as the presence of mycorrhizal fungi (Scagel 2004), also has an effect on the ability to produce flowering scapes, scape size, and the number of flowers (Han et al. 1991; Schlising and Chamberlain 2006). Corm size also appears to have an effect on these characters in *Dichelostemma capitatum* (unpublished observations). Leaf width appears to be positively correlated with corm size in both *D. capitatum* and *D. lacuna-vernalis*, and the observation of smaller leaf widths in *D. lacuna-vernalis* (Table 1) may be due, at least in part, by the ability of *D. lacuna-vernalis* to flower from smaller corms. The influence of corm size on reproductive traits in *D. capitatum* and *D. lacuna-vernalis* is currently under investigation and will be the subject of a forthcoming paper.

The results of the morphological analysis and the common garden study both support Lenz’ (1974) proposal that as *D. lacuna-vernalis* merits taxonomic recognition. As the DA showed, *D. lacuna-vernalis* plants can be distinguished from *D. capitatum* plants with a high degree of reliability, and the populations can be easily recognized in the field by characteristics other than the small stature and few-flowered scapes (Table 4). Less clear, however, is whether it should be recognized at species rank or at an infraspecific rank.

Taxonomic circumscriptions within Brodiaeoideae traditionally have been grounded on the morphological species concept, with species distinguished on the basis of discrete differences in the shape of the floral parts and with infraspecific taxa delineated on the basis of size differences or the relative position of floral parts treated (Hoover 1939, 1940, 1941; Preston 2010). *Dichelostemma lacuna-vernalis* is distinguished

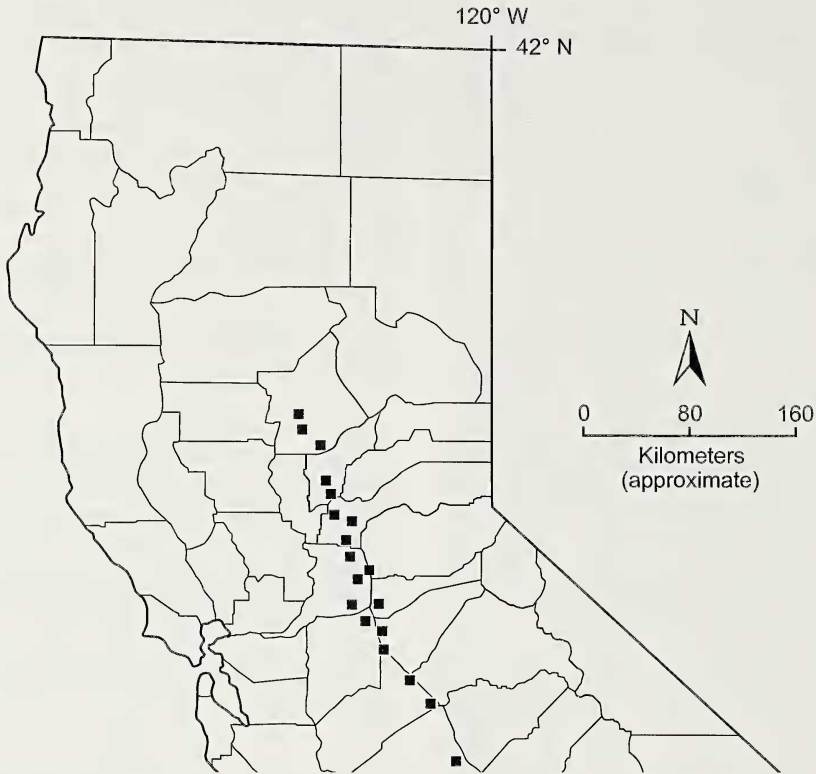


FIG. 5. Distribution of *Dichelostemma capitatum* subsp. *lacuna-vernalis* in California, USA.

from *D. capitatum* primarily on the basis of size differences (scape height, flower number, and the size of the floral parts), which suggests treating *D. lacuna-vernalis* as an infraspecific taxon. Evidence for treating *D. lacuna-vernalis* at species rank, i.e., reproductive barriers between *D. lacuna-vernalis* and *D. capitatum* as a consequence of genetic or ecological factors, or both, is currently ambiguous. Although *D. capitatum* is known to consist of multiple cytotypes (Keator 1968), no chromosome counts for *D. lacuna-vernalis* have been documented, and no hybridization studies have been done. Under current practice, infraspecific taxa in Brodiaeoideae are recognized as subspecies (Niehaus 1971; Keator 1991; Pires 2002a, b; Pires and Keator 2012, Pires and Preston 2012); therefore, *D. lacuna-vernalis* appears to be best treated at subspecies rank. Taylor (2010) independently came to the same conclusion and proposed the new combination, *Dichelostemma capitatum* subsp. *lacuna-vernalis* (L.W. Lenz) D.W. Taylor.

The morphometric analysis unexpectedly found that populations of *D. capitatum* sampled for this study also form two distinct groups, one of which shared some characteristics with *D. lacuna-vernalis* and shared other characteristics with “typical” *D. capitatum*, with some characteristics appearing intermediate (Figs. 1–4). The 22 populations of *D. capitatum* in Group 2a

(C22–C43) are recognizable statistically (cluster analysis, PCA) as well as by distinct morphological characteristics, such as the decurrent bases of the outer perianth lobes (Fig. 3). The populations appear to have a discrete geographic distribution, although this has not been fully investigated. Most of the populations (C22–C36) occur along the western base of the Sierra Nevada foothills parapatrically with *D. lacuna-vernalis* (sympatric in at least one location) or at higher elevations than *D. lacuna-vernalis*. Other populations in Group 2a (C37–C43) occur in the interior North Coast Ranges outside of the range of *D. lacuna-vernalis*. The interior North Coast Range populations are similar to the Sierra Nevada foothill populations in most characteristics but have smaller flowers.

The results of this study indicate that other population groups in *D. capitatum* can be distinguished morphologically and geographically and may merit taxonomic consideration. However, a number of questions remain to be addressed before formal taxonomic recognition of these groups can be proposed. What is the geographic extent of the Group 2a populations? Because the distinctiveness of these populations was not recognized before this study, the full distribution of these populations has not been determined or sampled, as has been the case for *D. lacuna-vernalis*. Keator (1968) noted that *D.*

capitatum populations in southern California mountains have small flowers, and these populations also need to be evaluated. Do these other morphologically recognizable groups correspond to different cytotypes? Keator's (1968) finding that diploids have smaller flowers than polyploids suggests that this may be the case, but additional cytological studies are needed to evaluate that hypothesis. Studies utilizing DNA markers are needed to test the validity of the morphologically recognizable groups and may be needed to determine whether the polyploid cytotypes represent unique lineages or multiple lineages. *Dichelostemma capitatum* is a common and familiar member of the California flora, but such familiarity appears to have fostered an assumption that the species has been well-characterized.

TAXONOMIC TREATMENT

***Dichelostemma capitatum* (Benth.) Alph. Wood** subsp. *lacuna-vernalis* (L.W. Lenz) D.W. Taylor, Fl. Yosemite Sierra 373. 2010. *Dichelostemma lacuna-vernalis* L.W. Lenz, Aliso 8: 129. 1974.—TYPE. USA, California, Sacramento Co., Orangevale, 12 Apr 1967, L.W. Lenz 24671a (holotype: RSA235779 [digital image!]; isotypes: RSA235800, RSA457167, RSA457168, RSA457169, RSA457170, RSA457171 [digital images!]).

Because the original description was based solely on the type specimen, the description for *D. capitatum* subsp. *lacuna-vernalis* is emended here to incorporate data obtained from populations sampled across the range of the subspecies.

Perennial herb from a corm; corms up to 25 mm in diam, not deeply seated, sometimes bearing 1–2 offsets. Leaves 2, subulate, thin, flat to concave, keel-less, ca. 2 dm long, 2.2–8.8 (–12.5) mm broad at base, margins ciliate. Inflorescence scapose, umbellate, 1–3(–5) flowered; scape 1–4(–6) per corm, slender, (4.4–) 6.2–22.6 (–26.1) cm long; bracts ca. 6 mm wide, (4.8–) 6.2–13.5 (–16.0) mm long, ovate, acuminate, purple; pedicels < 4.4 (<6.0) mm long. Flowers blue-violet; perianth (9.8–) 10.7–16.6 (–17.8) mm long; tube campanulate, (2–) 2.4–4.8 (–6.0) mm long; outer lobes ovate, cordate at base, (7.5–) 9.0–13.8 (–14.6) mm long, (4.0–) 4.9–9.3 (–9.8) mm wide; inner lobes oblong, (6.3–) 7.6–12.3 (–13.3) mm long, (3.2–) 4.0–7.9 (–9.0) mm wide; appendages (3–) 3.7–6.0 (–6.7) mm long; outer stamens (2.8–) 3.2–5.4 (–5.6) mm long, filaments (1.5–) 1.6–3.5 (–3.8) mm long, anthers (1.2–) 1.5–3.5 (–3.0) mm long; inner stamens (2.9–) 3.0–4.9 (–5.2) mm long, filaments (0.5–) 0.7–2.5 (–2.8) mm long, anthers (1.7–) 2.4–4.3 (–4.5) mm long; ovary ovoid, (2.0–) 2.5–4.5 (–5.0) mm long; style (2.5–) 2.8–5.0 (–6.5) mm long; ovules (7–) 8–17

(–20) per locule. Fruit a loculicidal capsule, ovoid, ca. 8.5 mm long, 5.5 mm wide, valve apex acute. Seeds black, ovoid to rhomboid, finely striate, 1–1.5 mm long.

Phenology

Like many other geophytes in the Brodiaeaceae (Niehaus 1971; Han et al. 1994; Schlising and Chamberlain 2006; Kannely and Schlising 2014), *D. capitatum* subsp. *lacuna-vernalis* forms corms that are dormant in the soil during the summer drought. New leaves emerge soon after the start of the rainy season, generally in October or November. The plants spend the next three to four months producing a new main corm. Blooming in the field occurs from late February to early April, generally two to three weeks sooner than sympatric populations of *D. capitatum* subsp. *capitatum*. However, plants grown in pots in Davis, California, bloomed as early as the first week of January. Seed set follows soon after, and all aboveground parts wither and dry during the summer dormant period. Because the corms produce few offsets, and the subspecies appears to reproduce primarily by seed.

Distribution and Ecology

Dichelostemma capitatum subsp. *lacuna-vernalis* is endemic to the western base of the Sierra Nevada foothills and adjacent Great Valley, ranging from Butte County south to Merced County (Fig. 5). The populations are restricted to a narrow elevation band between 30 and 270 m, which corresponds to the zone of annual precipitation between the 500 and 750 mm isohyets (National Weather Service 2013). Based on soil information obtained for each population from the National Resource Conservation Service's Web Soil Survey (<http://websoilsurvey.nrcs.usda.gov/>), soils in which the populations occur are loamy, usually sandy loams, gravelly loams, or stony loams, most of which are alfisols (Redding, Red Bluff series), enceptisols (Exchequer series), and ultisols (Mokelumne series). These soils formed in alluvium from mixed sources and are shallow, having a duripan, bedrock, or both present within 0.25 to 1.5 m of the soil surface.

The epithet "*lacuna-vernalis*" refers to the undulating vernal pool-swale terrain in which the species often occurs (Lenz 1974); however, the populations do not grow in vernal pools but in open upland grasslands adjacent to vernal pools, often on mounds, or in grassy swales in oak woodland. Associated species are early spring blooming annuals, including *Amsinckia menziesii* (Lehm.) Nelson & J.F. Macbr., *Minuartia californica* (A. Gray) Mattf., *Crassula connata* (Ruiz-Lopez & Pavon), *Dichelostemma capitatum*

subsp. *capitatum*, *Dichelostemma multiflorum* (Benth.) A.A. Heller, *Erodium botrys* (Cav.) Bertol., *Eschscholzia lobbii* Greene, *Hypochaeris glabra* L., *Lasthenia gracilis* (DC.) Greene, *Layia fremontii* (Torr. & A. Gray) A. Gray, *Lepidium nitidum* Torr. & A. Gray, *Lomatium* spp., *Lupinus bicolor* Lindley, *Minuartia californica* (A. Gray) Mattf., *Plagiobothrys* spp., *Plantago erecta* E. Morris, *Senecio vulgaris* L., *Thysanocarpus radians* Benth., *Trifolium depauperatum* Desv., *Triphysaria eriantha* (Benth.) Chuang & Heckard, and *Triteleia hyacinthina* (Lindley) Greene.

Conservation Status

Shortly after it was described, *D. capitatum* subsp. *lacuna-vernalis* was included in the California Native Plant Society (CNPS) Inventory of Rare and Endangered Plants of California as "rare and endangered" (Smith et al. 1980). It was reviewed by the U.S. Fish and Wildlife Service as a candidate for listing under the Endangered Species Act, but after the discovery of additional occurrences in the early 1980's, it was determined not to be threatened or endangered, and subsequent editions of the CNPS Inventory listed it as "rare, but not endangered." It was dropped entirely from the CNPS Inventory after being synonymized with *D. capitatum* in the first edition of *The Jepson Manual* (Keator 1993).

Based on current herbarium records, *D. capitatum* subsp. *lacuna-vernalis* is known from only 40 occurrences. Because it has a relatively broad range (285 km) that spans most of the length of the Sacramento Valley and the north end of the San Joaquin Valley, and because the plants appear to be locally common where present, it should not currently be considered rare. However, because it occurs within a narrow elevation band, it has a very limited distribution. Moreover, it occurs within an area that is experiencing substantial population growth, which makes it vulnerable to future habitat loss, and at least three of the known occurrences are located in urbanized areas and appear to have been extirpated (personal observation). Therefore, *D. capitatum* subsp. *lacuna-vernalis* should be considered a "watchlist" plant (California Rare Plant Rank 4) by the California Natural Diversity Database.

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I am grateful to Craig Martz (California Department of Fish and Game) for sharing his field notes and unpublished reports from his files. Without his earlier efforts of to locate and document populations of *D. lacuna-vernalis*, this study would have been much more difficult to carry out. I also thank three anonymous reviewers for constructive criticism of the manuscript.

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APPENDIX 1

VOUCHER SPECIMENS FOR POPULATIONS SAMPLED FOR MORPHOLOGICAL MEASUREMENTS. CHARACTERS MEANS ARE PROVIDED IN APPENDIX 2.

Dichelostemma capitatum. C01: Butte Co., Upper Bidwell Park, Chico, on the north rim at the level of Horseshoe Lake, 09 Feb 1983, *Oswald 63* (CHSC). C02: Placer Co., 4 mi E of Lincoln, 16 Mar 2013, *Preston 2891* (DAV). C03: Sacramento Co., Fair Oaks, Phoenix Park, 14 Mar 2009, *Preston 2653* (DAV). C04: Sacramento Co., along Scott Rd, ca. 0.5 mi N of its jct with Latrobe Rd, 03 Apr 2010, *Preston 2738* (DAV). C05: Sacramento Co., along Scott Rd, 1.6 mi S of its jct with White Rock Rd, 03 Apr 2010, *Preston 2736* (DAV). C06: Sacramento/Amador Co., ca. 5.5 mi W of Ione, along Hwy 104, 24 Mar 2013, *Preston 2899* (DAV). C07: Calaveras Co., 1.7 mi NNE of Burson, along Chile Camp Rd, at jct with S Camanche Parkway, 08 Apr 2007, *Preston 2424* (DAV). C08: San Joaquin Co., 5 mi NE of Bellota, along Hwy 26, 15 Apr 2007, *Preston 2426* (DAV). C09: Calaveras Co., 5 mi NW of Copperopolis, along Salt Springs Valley Rd, 0.15 mi S of jct with Rock Creek Rd, 15 Apr 2007, *Preston 2429* (DAV). C10: Napa Co., along Hwy 128, 0.4 mi W of Knoxville Rd, 14 Apr 2013, *Preston 2904* (DAV). C11: Colusa Co.; along CA-20, 9.7 miles southwest of Williams, on the north side of Salt Creek, 11 Mar 2009, *Helmkamp and Helmkamp 14366* (UCR). C12: Solano Co., ca. 4 mi NE of Benicia, along Lopes Rd, 0.7 mi N of its jct with Parish Rd, 22 Mar 2013, *Preston 2897* (DAV). C13: Alameda Co., Mission Hills, 0.4 mi SW of Ohlone College, 22 Mar 2013, *Preston 2896* (DAV). C14: Santa Clara Co., Anderson Lake County Park, 22 Mar 2013, *Preston 2895* (DAV). C15: San Mateo Co., Hillsborough, along Crystal Springs Rd where it crosses under the Junipero Serra Freeway, 28 Mar 2013, *Preston 2900* (DAV). C16: Stanislaus Co., mouth of Arroyo Del Puerto, 28 Mar 1935, Sharsmith 1532 (UC). C17: Fresno Co., along Panoche Rd, 2.5 mi W of Interstate 5, 24 Mar 2009 [voucher misplaced, to be recollected]. C18: Fresno Co., 9.5 mi NE of Coalinga, at Skunk Hollow, 24 Mar 2008 [voucher misplaced, to be recollected]. C19: Fresno Co., Clovis, at jct Herndon Ave and Academy Ave, 01 Apr 2013, *Preston 2901* (DAV). C20: Fresno Co., Friant, along

Millerton Rd, across from entrance to Friant Dam, 01 Apr 2013, *Preston 2902* (DAV). C21: Kern Co., Tehachapi Mtns, ca. 9.3 mi ENE of Lebec, in Bear Trap Canyon, 15 May 2007, *Preston 2515* (DAV). C22: Butte Co., top of North Table Mt., W edge of Mountain adjacent to the waterfall at the S branch of Coal Creek, 23 Feb 1979, *Jokerst 1134* (CHSC). C23: Butte Co., Table Mountain, 0.2 mi SE of Cherokee Rd, 16 Mar 2013, *Preston 2894* (DAV). C24: Butte Co., 7.9 mi NNE of Oroville, along E side of Clark Rd, 16 Mar 2013, *Preston 2893* (DAV). C25: Yuba Co., along both sides of Hammonton-Smartville Rd, 1.0 mi E of N entrance to Beale AFB, 25 Mar 1982, *Martz & Sanner 42* (DAV). C26: Sacramento Co., E of Rancho Cordova, along Scott Rd, 1.2 mi S of its jct with White Rock Rd, 24 Mar 2013, *Preston 2898* (DAV). C27: Sacramento Co., along Scott Rd, 0.95 mi S of Deer Creek, 03 Apr 2010, *Preston 2737* (DAV). C28: Sacramento Co., along Hwy 16, at jct with Ione Rd, 22 Mar 2014, *Preston 2949* (DAV). C29: Sacramento Co., along Ione Rd, 2.35 mi S of Hwy 16, 03 Apr 2010, *Preston 2739* (DAV). C30: Amador Co., 2.5 mi NW of Ione, along Irish Hill Rd, 0.56 mi N of Hwy 104, 08 Apr 2007, *Preston 2422* (DAV). C31: Amador Co., 1.9 mi SSE of Ione, along Buena Vista Rd, 0.1 mi S of jct with Hwy 88, 08 Apr 2007, *Preston 2423* (DAV). C32: Sacramento Co., Rancho Seco County Park, 06 Apr 2014, *Preston 2950* (DAV); C33: Calaveras Co., 1.4 mi NNE of Burson, along Chile Camp Rd, 0.7 mi E of Burson Rd, 17 Apr 2010, *Preston 2763* (DAV). C34: San Joaquin Co., 3.8 mi E of Clements, on W side of Cord Rd, 0.9 mi S of jct with Hwy 12, 15 Mar 2008, *Preston 2587* (DAV). C35: Calaveras Co., 0.75 mi SE of Wallace, on S side of Hwy 12, 22 Mar 2014, *Preston 2948* (DAV). C36: Stanislaus Co., north side of Tuolumne River, opposite La Grange, 22 Feb 1941, Hoover 4773 (UC). C37: Lake Co., SE edge of Manning Flat, 03 May 2011, *Preston 2856* (DAV). C38: Lake Co., Shaul Valley, in field N of SR 29, 04 May 2011, *Preston 2857* (DAV). C39: Napa Co., Lake Hennessy, along Conn Valley Rd at public access site, 16 Apr 2013, *Preston 2907* (DAV). C40: Sonoma Co.,

0.6 mi E of Occidental, at jct Occidental Rd and Facendini Lane, 29 Mar 2013, *Preston 2901* (DAV). C41: Napa Co., Calistoga, E end of old landing strip, on N side, 16 Apr 2013, *Preston 2905* (DAV). C42: Lake Co., 4.5 mi NW of Middletown, on W side of Hwy 175, 16 Apr 2013, *Preston 2908* (DAV). C43: Lake Co., Kelseyville, at SW corner of jct Main St and Douglas Rd, 16 Apr 2013, *Preston 2909* (DAV).

Dichelostemma lacuna-vernalis. L01: Butte Co., E side of State Route 191 at intersection of Pentz Rd, 22 Mar 1982, *Martz 30* (DAV). L02: Butte Co., ca. 3.7 mi NW of Oroville, on NW side of PG&E substation, 23 Mar 2007, *Preston 2418* (DAV). L03: Butte Co., along State Route 70, 1 mi N of intersection with Palermo Rd, S of Oroville, 16 Mar 1982, *Martz 31* (DAV). L04: Yuba Co., along Hammonton-Smartville Rd, 2.4 mi E of Doolittle Drive, 16 Mar 2013, *Preston 2892* (DAV). L05: Placer Co., both sides of Dowd Rd, 3 mi S of Sheridan, 24 Mar 1982, *Martz 41* (DAV). L06: Yuba Co., along both sides of Wheatland-Smartville Rd, 3.7 mi NE of Wheatland, 26 Mar 1982, *Sanner 33* (DAV). L07: Placer Co., west side of Sierra College Blvd, 1.1 miles S of English Colony Rd intersection, 26 Mar 1982, *Martz 38* (DAV). L08: Placer Co., on Sierra College Blvd, 2.3 mi N of Douglas Blvd intersection, 07 Mar 1982, *Martz 13* (DAV). L09: Sacramento Co., Fair Oaks, Phoenix Park, 31 Mar 2007, *Preston 2419* (DAV). L10: Sacramento Co., W side of Scott Rd, 1.2 mi S of intersection with White Rock Rd, 26 Mar 1982, *Martz 36* (DAV). L11: Sacramento Co., E side of Scott Rd, 1.6 mi N of intersection with Latrobe Rd, 26 Mar 1982, *Martz 35* (DAV). L12: Sacramento Co., on E side of Ione Rd, 2.3 mi S of jct with Hwy 16, 12 Mar 2008, *Preston 2586* (DAV). L13: Amador Co., 0.7 mi W of Indian Hill, along S side of Hwy 104, 02 Apr 2007, *Preston 2420* (DAV). L14: Calaveras Co., 0.75 mi SE of Wallace, on S side of Hwy 12, 15 Mar 2008, *Preston 2588* (DAV). L15: Calaveras Co., W side of County Rd J14 (Milton Rd), 1.3 mi N of intersection with Hunt Rd, 10 Mar 1982, *Martz 21* (DAV). L16: Merced Co., ca. 5 mi NE of Planada, at jct Cunningham Rd and S Bear Creek Drive, 09 Mar 2010, *Preston 2721* (DAV).

APPENDIX 2

POPULATION MEANS

Means for 19 morphological characters measured in field-collected individuals of *Dichelostemma capitatum* (43 populations) and *D. lacuna-vernalis* (16 populations). Population codes and vouchers are provided in Appendix 1. Characters: 1 = scape height; 2 = leaf width; 3 = flowers/scape; 4 = bract length; 5 = pedicel length; 6 = perianth length; 7 = perianth tube length; 8 = outer lobe length; 9 = inner lobe length; 10 = outer lobe width; 11 = inner lobe width; 12 = appendage length; 13 = outer filament length; 14 = inner filament length; 15 = outer anther length; 16 = inner anther length; 17 = ovary length; 18 = style length; 19 = ovules/ovary. Measures are in mm, except scape height (cm).

		Characters																		
Taxon	Population code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Dichelostemma capitatum</i>																				
	C01	26.7	8.3	5.4	17.5	5.3	17.5	6.6	12.0	10.9	5.8	6.6	7.2	3.1	2.2	2.8	4.7	4.7	7.5	29.9
	C02	31.6	9.9	9.4	18.9	8.5	16.0	6.3	10.1	9.7	5.3	5.8	6.1	2.7	2.0	2.5	4.2	4.6	5.4	38.7
	C03	40.7	7.8	5.5	16.0	6.1	16.6	6.1	11.2	10.5	5.3	5.9	6.8	2.7	2.0	2.6	4.2	4.6	6.4	31.8
	C04	41.1	7.7	6.8	14.4	8.1	15.8	5.5	10.8	10.3	4.8	5.5	5.6	2.7	1.6	2.2	3.8	4.3	5.5	36.0
	C05	35.7	7.0	6.8	14.8	6.7	16.7	6.2	11.0	10.5	4.9	5.6	6.7	2.9	2.0	2.5	4.2	4.3	6.3	30.9
	C06	24.6	6.9	5.5	14.2	5.8	14.7	5.4	9.9	9.3	4.9	5.5	6.2	2.4	1.6	2.3	4.1	4.0	4.9	40.2
	C07	35.6	6.3	4.2	13.2	5.0	14.6	5.6	9.5	9.0	4.3	4.7	5.8	2.5	1.6	2.2	3.7	3.9	5.2	38.8
	C08	39.8	8.1	7.4	14.2	7.0	15.6	5.5	10.4	10.2	4.9	5.7	6.2	2.5	1.6	2.5	4.2	4.5	4.9	42.0
	C09	39.3	8.0	9.8	16.0	9.6	15.1	5.5	10.2	9.7	5.3	6.1	6.3	2.8	1.9	2.3	3.9	4.4	5.0	36.4
	C10	28.9	7.7	5.9	14.9	5.8	14.4	5.7	9.2	8.7	5.0	5.7	6.3	2.6	2.0	2.4	3.9	4.1	5.4	27.8
	C11	37.5	7.9	6.7	16.9	6.8	16.9	6.9	10.7	10.0	5.5	6.2	7.3	3.2	2.7	2.6	4.3	4.8	7.2	29.5
	C12	34.3	8.6	8.1	18.0	5.9	17.5	6.8	10.9	10.7	6.0	6.6	7.5	3.3	2.5	2.6	4.5	4.8	7.1	33.3
	C13	24.5	6.4	5.2	18.5	5.5	17.4	7.1	11.0	10.3	5.5	6.0	6.8	2.9	2.3	2.4	4.1	4.4	7.7	33.1
	C14	32.1	9.0	6.9	16.2	8.7	17.4	7.5	10.6	9.8	5.2	5.8	6.9	2.5	2.1	2.2	4.0	4.8	6.9	28.6
	C15	29.5	6.5	7.2	12.6	5.3	17.7	8.1	11.6	9.6	4.3	4.7	6.2	2.0	1.3	2.5	4.2	4.3	7.8	19.4
	C16	33.9	6.6	5.1	14.0	5.7	16.6	6.8	10.6	9.8	5.4	6.2	6.6	2.5	2.1	2.5	4.1	4.8	6.7	30.5
	C17	33.2	8.7	8.9	15.0	8.2	15.8	6.4	10.2	9.4	5.1	5.8	6.3	2.4	1.7	2.5	4.1	4.6	6.3	36.6
	C18	36.3	11.3	10.1	13.5	8.7	16.3	7.1	10.0	9.2	4.9	5.4	5.9	2.6	2.0	2.4	3.9	4.5	5.7	34.0
	C19	43.3	10.0	7.3	17.0	6.9	16.2	6.8	10.0	9.4	4.9	5.4	6.7	2.9	2.2	2.4	4.4	4.6	6.3	35.3
	C20	35.7	9.2	8.2	15.2	8.3	15.6	6.2	10.0	9.4	4.9	5.4	6.2	2.3	1.9	2.2	3.9	4.3	5.5	39.0
	C21	—	—	9.7	13.2	4.8	13.9	5.8	—	8.2	3.6	4.3	4.8	1.9	1.0	2.2	3.5	3.8	4.8	22.7
	C22	18.4	7.3	3.7	14.8	5.7	16.8	5.9	12.7	10.8	5.6	5.8	6.1	2.6	1.6	2.6	4.2	4.1	6.8	25.1
	C23	13.4	6.8	3.3	14.3	4.6	16.8	6.4	12.3	10.4	5.5	5.5	5.9	2.5	1.4	2.3	3.7	3.7	6.0	24.6
	C24	28.4	7.6	2.9	11.7	3.8	16.9	5.5	13.1	11.4	5.5	5.7	6.5	2.6	1.5	2.7	4.1	3.7	7.9	23.4
	C25	15.7	5.5	1.4	10.2	2.4	17.5	5.1	14.5	12.4	6.8	6.3	6.4	2.9	1.8	2.9	4.2	4.0	6.1	30.8
	C26	21.8	5.1	2.6	10.9	3.1	16.3	5.2	13.1	11.1	5.9	5.6	6.3	2.6	1.6	2.3	3.7	3.8	6.3	28.1
	C27	18.9	3.7	2.2	9.6	2.5	15.2	5.0	12.4	10.2	5.3	5.0	5.7	2.3	1.2	2.3	3.7	3.3	5.7	28.8
	C28	26.6	5.5	2.7	10.5	2.8	16.1	5.4	11.6	10.7	5.6	5.4	6.0	2.4	1.2	2.3	3.6	3.7	6.5	27.2
	C29	23.9	4.6	2.1	9.2	2.8	16.1	5.6	12.1	10.5	5.9	5.5	5.7	2.2	1.2	2.3	3.6	3.9	6.0	25.8
	C30	28.5	4.9	2.7	9.9	2.7	17.0	5.7	12.9	11.3	5.9	5.6	5.9	2.3	1.3	2.2	3.6	3.6	5.9	27.4
	C31	25.4	4.7	3.1	9.7	2.8	15.6	5.7	11.2	9.9	5.2	5.1	5.5	2.1	1.1	2.1	3.5	3.5	6.3	23.8
	C32	20.0	5.5	2.8	11.5	3.9	16.1	5.6	12.7	10.5	5.8	5.2	6.0	2.4	1.6	2.8	4.5	3.7	6.4	24.4
	C33	25.8	5.3	3.5	9.7	2.6	16.2	5.8	12.2	10.4	4.9	4.9	5.7	2.1	1.2	2.3	3.5	3.4	6.3	26.8
	C34	18.0	8.3	3.3	13.5	5.0	16.5	6.3	11.9	10.2	6.0	6.2	6.4	2.6	1.5	2.3	3.9	3.9	6.5	26.4
	C35	34.0	10.3	4.4	15.1	5.1	18.2	7.1	13.1	11.1	7.0	6.9	6.7	2.7	1.7	2.5	3.8	4.1	7.6	30.9
	C36	16.7	4.6	2.8	10.9	2.7	14.8	5.7	11.3	9.1	5.4	5.3	5.6	2.6	1.4	2.2	3.6	3.5	6.1	26.3
	C37	20.5	5.4	3.0	10.6	3.2	14.1	5.3	10.2	8.8	5.1	5.4	5.3	2.2	1.4	2.4	3.7	3.9	5.1	20.9
	C38	16.0	5.3	2.1	9.3	3.0	12.4	4.5	9.5	7.8	5.5	5.4	4.4	2.1	1.1	2.0	3.2	3.2	4.1	23.1
	C39	24.3	12.7	3.7	11.5	4.1	12.9	4.6	9.6	8.3	5.4	5.8	4.6	2.6	1.5	2.2	3.3	3.9	4.3	32.5
	C40	13.0	5.4	2.2	9.9	2.5	13.5	4.0	10.7	9.5	5.9	5.7	4.9	2.4	1.5	2.2	3.6	3.7	4.1	27.7
	C41	22.2	7.4	2.9	12.5	4.4	14.6	4.9	11.3	9.8	5.4	5.3	5.2	2.9	1.7	2.3	3.8	4.0	4.8	28.4
	C42	22.9	6.0	2.9	11.4	3.2	14.3	5.4	11.1	8.9	5.6	5.4	5.4	2.7	1.7	2.3	3.7	3.5	5.2	24.7
	C43	17.2	7.7	3.9	12.1	3.6	14.1	4.9	11.2	9.2	5.8	5.5	5.4	2.4	1.3	2.3	3.5	3.8	4.8	27.8
<i>Dichelostemma lacuna-vernalis</i>																				
	L01	7.5	3.9	1.8	11.0	2.8	12.6	4.1	9.8	8.4	5.4	4.7	4.3	2.2	1.5	2.0	3.1	3.0	3.8	30.5
	L02	13.7	5.0	1.7	11.3	2.8	14.4	3.6	12.1	10.8	7.7	6.9	5.1	2.9	2.1	2.2	3.4	3.7	4.3	32.7
	L03	16.8	4.6	1.1	11.0	2.0	13.7	3.5	11.7	9.9	6.5	5.6	4.9	2.7	1.8	2.2	3.4	3.3	4.3	32.7
	L04	10.0	4.4	1.8	9.7	2.4	12.1	3.4	10.1	8.7	6.2	5.1	4.2	2.1	1.3	2.0	3.1	3.1	3.4	35.8
	L05	12.3	4.9	1.8	9.3	2.9	12.8	3.4	10.7	9.4	6.4	5.3	4.6	2.5	1.6	2.0	3.4	3.3	3.6	36.4
	L06	17.3	5.2	1.6	9.9	2.8	14.0	3.3	11.8	10.7	7.0	5.9	4.8	2.8	1.8	2.1	3.3	3.3	3.8	37.1

APPENDIX 2. CONTINUED.

Taxon	Population code	Characters																		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
	L07	15.5	6.9	2.2	11.8	3.7	15.0	4.1	12.3	11.0	8.1	6.9	5.4	3.1	2.1	2.4	3.7	4.1	4.5	42.7
	L08	16.6	6.7	2.1	10.1	2.9	14.0	3.4	12.1	10.6	7.2	6.2	5.0	2.8	1.7	2.2	3.5	3.5	4.0	39.1
	L09	12.2	4.4	1.4	8.4	1.8	13.1	3.0	11.2	10.1	7.2	5.9	4.9	2.6	1.7	2.0	3.2	3.3	3.6	34.8
	L10	13.0	5.1	1.6	9.8	2.4	13.8	3.6	11.7	10.1	7.2	6.1	5.1	2.6	1.8	2.1	3.4	3.3	3.9	41.6
	L11	13.2	4.4	1.4	8.3	2.3	13.2	3.6	11.0	9.6	6.9	5.6	4.8	2.5	1.6	2.1	3.4	3.6	3.7	40.4
	L12	16.9	5.7	1.4	9.5	2.3	14.4	3.9	12.1	10.5	7.7	6.2	5.0	2.6	1.5	2.3	3.7	3.6	4.0	44.3
	L13	16.3	4.5	1.9	8.3	2.3	13.6	3.5	11.1	10.1	6.4	5.0	4.6	2.7	1.4	2.1	3.2	3.2	3.6	43.8
	L14	13.9	6.6	1.6	9.0	2.4	13.7	3.9	11.4	9.9	7.7	6.4	4.9	2.6	1.5	2.0	3.3	3.7	3.8	39.0
	L15	17.0	5.0	1.7	10.2	2.9	14.6	4.1	12.0	10.5	7.8	6.3	5.1	3.0	1.7	2.3	3.6	3.8	4.1	42.8
	L16	16.3	6.2	1.7	9.4	2.3	12.2	3.0	10.7	9.2	6.6	5.5	4.7	2.4	1.5	2.1	3.3	3.2	3.7	37.8